

ECOLOGY AND LIFE HISTORY OF THE
RHYTIDOPONERA IMPRESSA GROUP
(HYMENOPTERA: FORMICIDAE)
II. COLONY ORIGIN, SEASONAL CYCLES,
AND REPRODUCTION

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INTRODUCTION

This paper is concerned with colony foundation and with seasonal cycles in brood composition and alate production in the *Rhytidoponera impressa* group, a species complex of ponerine ants restricted to rainforest and other mesic habitats in eastern Australia and New Guinea.

Life cycle information is most complete for *confusa* and *chalybaea*, and most of what follows refers to those species. Relevant data on the other three members of the *impressa* group (*enigmatica*, *impressa*, and *purpurea*) are given where available. When pertinent to the discussion, some observations on related *Rhytidoponera* species outside the *impressa* group are also included.

METHODS

Collection methods are described in Ward (1981). Most of the data are based on field observations and collections. Where appropriate, suspected reproductive females were dissected to ascertain the condition of the ovaries and spermatheca.

RESULTS

Colony origin

In the *Rhytidoponera impressa* group there are two methods by which colonies can originate:

- (i) from lone, colony-founding winged females (queens), in the manner characteristic of many ants; or

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Manuscript received by the editor April 15, 1981.

- (ii) as a result of colony fission or budding (hesmosis), in which one or more mated "workers", accompanied by uninseminated nest-mates, leave the parent colony to found a new daughter nest.

As the foregoing remarks imply, there are two kinds of reproductive females: queens and ergatoid (worker-like) gynes, the latter indistinguishable morphologically from unmated workers. This is the first record of reproductive workers in the *impressa* group (they are common and well-documented in some other *Rhytidoponera*) where previous reports suggested that the only functional reproductives were winged queens (cf. Brown, 1953, 1954; Haskins & Whelden, 1965). Mated queens and ergatoid gynes never coexist in the same nest, but they often occur in different nests in the same population (in *confusa*, *chalybaea* and *impressa*). This rather remarkable dimorphism of female reproductives in the *impressa* group and the resulting differences in colony structure and genetic relatedness will be examined in more detail elsewhere (Ward, in prep.).

There is little information on the frequency of colony fission in worker-reproductive colonies or on the size of newly-budded daughter colonies. Occasionally small isolated clusters of workers and brood are seen in the field, under stones or in rotten log cavities. Table 1 summarizes the composition of four such clusters in the *impressa* group, and two from other *Rhytidoponera* species (*tasmaniensis* and *fulgens*). Similar observations were made by Haskins & Whelden (1965) on *R. metallica*. Note that in the two cases where workers were dissected (Table 1), only one individual in each cluster was found to be inseminated. In no instance in the *impressa* group (or in any other *Rhytidoponera* species) was a single isolated worker, with brood, located in the field, in contrast to the frequent occurrence of single colony-founding queens (see below).

The process of colony fission is observationally difficult to distinguish from the movement of a colony from one nest site to another, and the two events may be inter-related. Table 2 summarizes observations made on colony movement in *chalybaea* and in three other *Rhytidoponera* species (outside the *impressa* group). In only one instance (*maniae*) was a single colony observed splitting into two nests, but the same event may have been occurring during the other observations, if some workers remained at the original nest site.

Table 1. Composition of small, isolated clusters of workers and brood (incipient worker-reproductive colonies?) in *Rhytidoponera confusa*, *chalybaea*, *tasmaniensis*, and *fulgens*.

Species	Locality	Date	No. workers	Brood
<i>confusa</i>	Royal Natl. Park, N.S.W.	5.xi.1974	5	eggs, larvae
"	Pearl Beach, N.S.W.	9.iv.1977	25*	9 eggs, 8 larvae
"	Seal Rocks, N.S.W.	14.vi.1977	13	several larvae
<i>chalybaea</i>	Whian Whian State Forest, N.S.W.	14.v.1977	9	several larvae
<i>tasmaniensis</i>	nr. Wonboyn Lake, N.S.W.	25.x.1975	6	none seen
<i>fulgens</i>	Mt. Koghis, New Caledonia	18.ii.1977	4*	several larvae, one worker cocoon

*workers dissected, one inseminated.

In view of the apparent scarcity of very small isolated clusters of workers and brood (of the size documented in Table 1, i.e. 5–25 workers), it seems likely that colony fission in the *impressa* group often produces daughter colonies larger in size. (Mature worker-reproductive colonies, i.e. those with alates, contain, on average, about 150 workers.) More field observations on budding are needed; the small amount of information accumulated thus far suggests that nocturnal observations might be rewarding. It is also possible that some worker-reproductive colonies develop from former queen-right colonies in which the queen has died.

The origin and development of queen-founded colonies in the *impressa* group has been more extensively documented. Incipient queen-right colonies have been observed repeatedly in the field (Table 3). Mated queens apparently disperse for some distance, undergo dealation, and search for a suitable nest site (under stones, rotting logs, etc.). Having located shelter, the queen excavates a small cavity, lays several eggs, and rears a small brood of workers, the first of these appearing within about 6 months (3–4 months in lab colonies). Unlike the claustral colony foundation typical of higher ants, queens forage outside the nest for food, and feed their larvae partly on insect prey.

The available field information on incipient, queenright colonies suggests that they are usually founded in the spring and early

Table 2. Field observations on colony movement and worker transport in *Rhytidoponera*.

Species	Date	Locality	Time (EDT)	Weather	Observations
<i>chalybaea</i>	13.i.1976	NSW: Sydney University	6.00 p.m.	cloudy, after raining much of the day	several workers transporting others to nest entrance (crack in sidewalk); all came from the same direction
<i>chalybaea</i>	28.ii.1976	NSW: Sydney University	6.30 p.m.	sunny period after raining most of the day	several instances of worker transport (and one of larval transport) from top of a stone ledge to a nest entrance on the side
<i>chalybaea</i>	6.iii.1977	NSW: Balgowlah, nr. Sydney	6.15-6.45 p.m.	mild, clear	workers carrying eggs, larvae, cocoons and other workers from one nest entrance at the base of a palm tree to another about a third of the way around the circumference, a distance of less than 1 meter
<i>victoriae</i>	28.xi.1976	NSW: Jct. of Kanagra Crk. & Cox's River	9.45-10.30 a.m.	overcast, mild	colony moving from one stone to another 1 meter distant; workers carrying egg clusters, larvae, cocoons, and other workers
<i>metallica</i>	10.i.1976	NSW: Gordon, nr. Sydney	2.30-3.30 p.m.	cloudy, following rainy period	workers transporting other workers (and in one instance a male) from one nest entrance (in soil) to another, 3 meters distant; worker transport still occurring the following day at 10.00 a.m.
<i>maniae</i>	1.xi.1975	NSW: 15 km N Coombah	c.9.00 a.m.	cloudy	workers carrying brood and other workers to one of two new nest sites, 0.6 and 2.5 meters, respectively, from old nest site, the directions at right angles to one another; all nests directly in soil

Table 3. Field data on 43 incipient, queenright colonies (with ≤ 20 workers). All *Rhytidoponera confusa* except the following accessions: 2006 (*chalybaea*), 2620 (*chalybaea*) and 2580 (*impressa*).

Accession no.	Population code no.	Date	Dealate Female(s)	Brood*				Probable year of origin
				Workers	Eggs	Larvae	Cocoons	
373	16	21.xi.74	1	5	0	+	0	1973
402	1	26.xi.74	1	2	0	+	+	1973
479	12	22.xii.74	1	14	+	+	+	1973
270	16	23.x.74	1	0	0	0	0	1974
273	16	23.x.74	1	0	0	0	0	1974
330	38	9.xi.74	1	0	0	0	0	1974
370	16	14.xi.74	1	0	+	0	0	1974
426	3	29.xi.74	1	0	+	0	0	1974
451	16	12.xii.74	1	0	+	0	0	1974
454	15	15.xii.74	1	0	-	-	-	1974
457	17	19.xii.74	1	0	+	+	0	1974
461	17	19.xii.74	1	0	+	+	0	1974
462	17	19.xii.74	1	0	+	+	0	1974
465	17	19.xii.74	1	0	-	-	-	1974
483	12	22.xii.74	1	0	-	-	-	1974
551	28	9.i.75	1	0	0	+	0	1974
552	28	9.i.75	1	0	+	+	+	1974
553	28	9.i.75	1	0	+	+	+	1974
554	28	9.i.75	1	0	0	+	0	1974
571	16	22.i.75	1	?	-	-	-	1974
580	13	22.i.75	1	0	0	+	+	1974
800	38	10.v.75	1	0	+	0	0	1974 or 1975
803	38	10.v.75	1	3	0	+	+	1974

Table 3 (continued).

Accession no.	Population code no.	Date	Deplete Female(s)	Workers	Brood*			Probable year of origin
					Eggs	Larvae	Cocoons	
808	38	10.v.75	1	?	-	-	-	1974
881	2	24.v.75	1	7	0	+	+	1974
970	34	13.vii.75	1	20	0	+	0	1974
1323	38	5.x.75	1	2	+	+	0	1974
1366	8	9.x.75	1	0	+	0	0	1975
1548	16	7.xii.75	1	0	+	0	0	1975
2020	25	5.xi.76	1	4	+	+	+	1975
1971	33	18.ix.76	1	0	0	+	0	1976
1988	30	2.x.76	1	?	-	-	-	1976
1996	30	3.x.76	2	0	0	0	0	1976
2006	57	4.x.76	1	0	0	0	0	1976
2022	25	5.xi.76	1	0	0	0	0	1976
2433	22	17.iv.77	1	0	0	0	0	1976 or 1977
2444	21	30.iv.77	2	0	0	0	0	1976 or 1977
2547	49	16.v.77	1	0	0	+	0	1976 or 1977
2472	39	11.v.77	1	12	+	+	0	1976
2580	93	9.vi.77	1	7	0	+	0	1976
2620	88	11.vi.77	1	17	0	+	0	1976
2849	30	8.x.77	1	0	+	0	0	1977
2850	30	9.x.77	1	0	+	0	0	1977

* brood: +, present; 0, absent; -, no information

Table 4. Composition of 322 *confusa* colonies, with respect to numbers of cocoons and alates, and month of collection. Large standard deviations are due to variation in colony size, and to the fact that not all nests produce alates in a given season.

Month	Sample Size (#colonies)	# worker cocoons mean \pm S.D.	# alate cocoons mean \pm S.D.	# alates mean \pm S.D.
Sept.	13	0.0 \pm 0.0	0.0 \pm 0.0	10.8 \pm 13.9
Oct.	47	0.2 \pm 0.5	0.0 \pm 0.0	5.3 \pm 12.7
Nov.	42	3.6 \pm 6.5	0.0 \pm 0.0	0.2 \pm 1.5
Dec.	13	16.3 \pm 27.7	5.7 \pm 14.6	0.1 \pm 0.3
Jan.	24	43.0 \pm 55.3	16.9 \pm 38.0	0.0 \pm 0.0
Feb.	10	62.8 \pm 40.1	15.9 \pm 15.7	1.0 \pm 2.8
Mar.	15	20.5 \pm 25.2	3.9 \pm 5.2	6.9 \pm 8.3
Apr.	26	27.5 \pm 32.5	1.8 \pm 4.4	23.1 \pm 29.9
May	41	0.4 \pm 1.2	0.0 \pm 0.0	12.7 \pm 21.4
June	50	0.1 \pm 0.3	0.0 \pm 0.0	25.5 \pm 39.0
July	32	0.0 \pm 0.0	0.0 \pm 0.0	25.0 \pm 29.7
Aug.	9	0.0 \pm 0.0	0.0 \pm 0.0	21.9 \pm 34.1

summer, and that development proceeds rather slowly. Of the 17 dealate females collected with eggs or no brood at all, 13 came from spring and early summer months (October–December) and only 4 from the fall (April–May) (Table 3). These findings are consistent with the observation that virgin alates usually remain in the nests throughout the winter, and fly in the spring. Nevertheless the occurrence of a few incipient colonies in apparently early stages of development in April and May requires some explanation: it seems likely that either development was hindered in these colonies or that occasional fall mating flights occur.

Colony foundation in the spring and early summer appears to be the pattern followed in *purpurea*: Brown (1954) noted many colony-founding dealate females of this species in October and November on the Atherton Tableland, north Queensland.

Forty-one of the 43 incipient colonies listed in Table 3 contained only a single queen. The two instances of primary pleometrosis (colony foundation by more than one queen) both involved colonies in a very early stage of development, without brood. One of these pairs (acc. no. 1996) was brought into the lab, and colony development was monitored. The two queens cohabited peacefully from 3 October, 1976 until the end of December, at which time the colony contained 12 eggs, 8 larvae and 8 worker cocoons. The first worker emerged 2 January, 1977; four days later (after a second

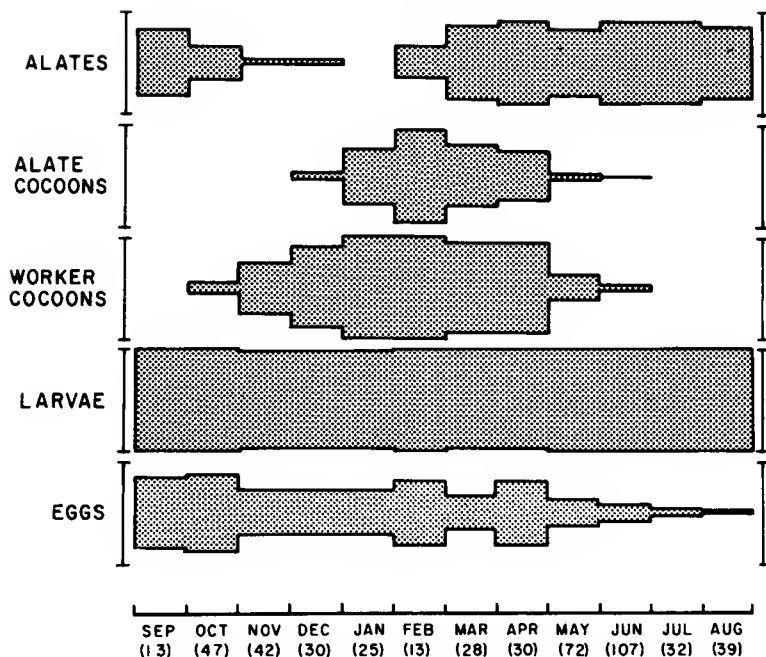


Figure 1. Seasonal changes in brood and alate composition in colonies of *confusa* and *chalybaea*, as measured by the proportion of colonies with various life stages. Maximum width (shown at either side of figure) indicates that 100% of colonies contain the particular stage. Because there were no obvious differences between species or between years, data covering both species over $3\frac{1}{2}$ seasons have been combined. Figures in parentheses refer to the number of colonies sampled in each month. Total sample size: 479 colonies.

worker had eclosed) one queen was found ousted from the nest and almost dead. The colony (with one remaining queen) continued to develop until artificially terminated 15 months later. Subsequent spermathecal dissections and electrophoretic analysis using allozyme markers confirmed that both females were inseminated, and that both had contributed worker offspring to the incipient colony.

Seasonal cycle in mature colonies

There are consistent seasonal patterns in the occurrence of brood and alates in mature colonies of the *impressa* group. These seasonal patterns are essentially the same for both queenright and worker-reproductive colonies, except that alates in the latter are pre-

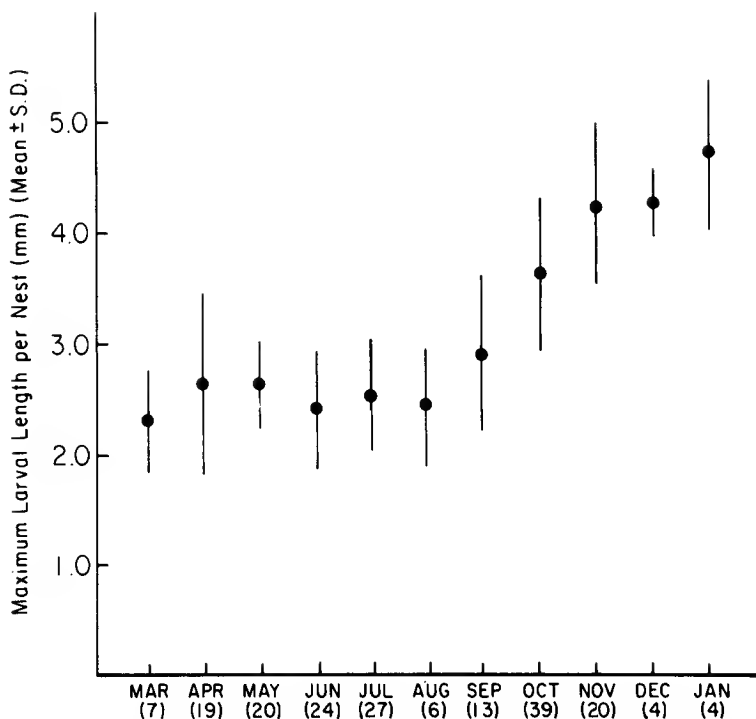


Figure 2. Maximum larval length per nest (measured in millimeters, with larva in natural resting position), in relation to time of year, for 183 nests of *confusa*. One larva (the largest) was measured in each nest. Figures in parentheses indicate the number of nests sampled. No data available for February.

dominantly male only. Figure 1 summarizes the seasonal changes for *confusa* and *chalybaea*, in terms of the proportion of colonies containing various stages of brood or alates, for each month. Data on absolute numbers of worker cocoons, alate cocoons, and alates are given in Table 4 for 322 *confusa* colonies (similar patterns are shown by *chalybaea*, but numbers average higher).

In *confusa* and *chalybaea* there appear to be two peaks of egg production—one in the spring (September–October) and another in the late fall (February–April). Larvae are continually present; those overwintering are small to medium-sized and show little growth until the spring, when development proceeds rapidly (Figure 2). Worker cocoons first appear in October–November, and not until

approximately two months later do the first alate cocoons appear (December–January). Adult workers emerge from January until June, while alates eclose over a shorter time period (February–April). Most, or all, of the alates overwinter in the nest, and are released in the spring, possibly in several bursts, since some nests have been found with alates as late as November (and one nest with a single male in early December).

Several points of interest emerge from the foregoing:

(1) There is only one crop of adults produced each year, and alate production is restricted to a limited period of the total time that new offspring are produced. At any given time, the standing crop of new cocoons consists on average of no more than about 30% alates (Table 4). These facts may be relevant to a consideration of control of the sex ratio of investment.

(2) No cocoons are overwintered, and there is a period of 6 months (July–December) when no new individuals are added to the workforce. At first glance, this would seem detrimental to the increased foraging requirements during rapid larval growth in the spring and early summer. However, because of a time lag between worker eclosion and foraging (callow workers remain in the nest) it may in fact produce an effective increase in the foraging force when it is most needed.

(3) In the absence of data on sex- and caste-specific growth rates, it is difficult to know whether alates arise from the overwintering larvae (hence, from eggs laid the previous season) or from eggs laid in the spring. However one piece of evidence suggests the latter: the discrepancy between the appearances of the first worker and first alate cocoons (two summer months) seems to be too great to be explained by assuming that equivalent-sized overwintering larvae require that extra period of time (and quantity of food) to develop into reproductives. Rather, it would seem more likely that the reproductives develop from spring-laid eggs or alternatively from smaller overwintering larvae.

Not all nests of *confusa* and *chalybaea* contain alates in a given season, alate production being associated with larger colony sizes (Table 5). Nevertheless, there is considerable overlap in colony size between nests with and without alates, partly due to the fact that worker-reproductive colonies produce alates at a smaller size (and probably younger age) than queenright colonies (Ward, 1978). It seems likely that a variety of genetic, environmental, and develop-

Table 5. Mean colony size (number of workers) for nests with alates and for those without alates at the time of year (February–September) when winged reproductives are normally present.

Species	Mean no. workers (\pm S.D.)	
	Alates present	Alates absent
<i>confusa</i>	203.1 \pm 179.9 (n=132)	83.9 \pm 65.7 (n=41)
<i>chalybaea</i>	270.7 \pm 206.2 (n=68)	146.7 \pm 122.4 (n=41)

mental (ergonomic) factors influence the production of alates.

The available information on *impressa* and *purpurea* indicates a seasonal brood cycle similar to that of *confusa* and *chalybaea*. Nests of the two former species collected in the winter in Queensland generally had small larvae (sometimes eggs), alates, and few or no cocoons (sample of 8 *impressa* colonies, 16 *purpurea* colonies). A lowland population of *purpurea* from near Cape Tribulation, north Queensland, was exceptional in overwintering with mature larvae, as well as worker cocoons and adult alates. Nothing is known of the brood cycle in New Guinea populations of *purpurea* which inhabit much less seasonal environments.

Thus, in Australia at least, four species in the *impressa* group produce one brood of sexuals a year, most or all of which are overwintered in the nest and released in the spring. This occurs *despite* contrasting climatic regimes at the north-south extremes of range (summer rainy season in the north, and winter rains in the south) (cf. Brown, 1954).

Collections of *enigmatica* suggest a similar brood cycle (i.e. small, overwintering larvae; cocoons present only in summer), with one important distinction: alates are usually absent from nests in the winter. Of 13 nests collected in the early winter (April 30–July 1) only one contained alates (all males); on the other hand, four out of five nests collected in the summer (January 12–March 7) contained alate pupae (also all males). The differences are significant ($p < .02$, two-tailed Fisher's exact test), and suggest that alates fly principally in the fall. If this is so, there would appear to be considerable temporal isolation between *enigmatica* and its two sympatric congeners (*chalybaea* and *confusa*).

Mating Flights

Two pieces of indirect evidence suggest that reproductives of *confusa* and *chalybaea* normally mate in the spring:

- (i) the proportion of nests containing alates is more or less constant throughout the late summer, fall and winter, dropping rapidly in the spring; and
- (ii) there is a flush of colony-founding females in the early to mid-summer. To the extent that *impressa* and *purpurea* share the same seasonal cycle, it may be supposed that their nuptial flights also occur in the spring.

Alates of *confusa* and *chalybaea* were observed actively dispersing or swarming on several occasions in rainforest and urban parkland in the Sydney region. All observations but one (out of 15) were made in the spring (September 15–November 10), and the only large-scale mating swarms were seen at this time. Most observations involved congregations of males around nest entrances. On six occasions, isolated male or female alates were observed away from the nest, apparently in a dispersing phase. Spring mating flights were observed for 3 consecutive years (1976–78) in the *chalybaea* population occurring on the University of Sydney campus. Because of the scarcity of information on this important stage of the life cycle, the 1976 mating swarm is described in detail.

This flight took place on 4 October 1976, a mild overcast day with brief periods of sunshine and light rain. At the time observations were begun (10:15 a.m. EST) large numbers of *chalybaea* alates, mostly males, were observed flying in parts of the University campus. Alates were distinctly concentrated into clusters in tree-shaded areas. Three of these concentrations were examined in detail (Sites A, B and C in Figure 3).

Site A. This cluster was centered about a *chalybaea* nest entrance between two slabs of sandstone which formed part of a stone wall. Between 10:45 and 11:45 a.m. there were several hundred males within 2 meters of the nest entrance. No alate females were seen. Although males spent most of the time on the ground chasing other individuals, the congregation appeared to be formed by males flying into the site. There were large numbers of workers milling around the nest entrance and most behaved aggressively towards the males, but this did not deter the latter from making repeated attempts to mate with workers (and with other males). Three apparently successful male-worker matings were observed; in each instance the pair was already in copulation when discovered, in a position similar to that described by Hölldobler & Haskins (1977) for *R. metallica*. The worker dragged the male on the ground for about 30

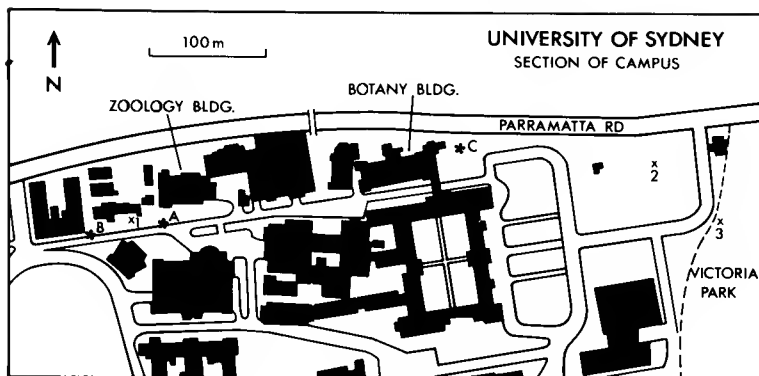


Figure 3. Section of University of Sydney campus where *chalybaea* nuptial flights were observed. A, B, and C represent sites of large clusters of alates, described in text. Lesser numbers of alates were observed at locations 1-3, and elsewhere.

seconds, after which separation occurred. Wings were vibrated rapidly during attempts by males to mount workers. A mating attempt by one male often attracted others, resulting in a buzzing, frolicking ball of males. Males were also observed to enter (and leave) the nest, and may perhaps have mated with workers within the nest. Several instances were noted of workers forcibly evicting males from the nest, dragging them to a distance of 1 meter from the nest entrance. Workers were still foraging during these events: two which were observed returning with a dead honey-bee, and another with a seed, were unmolested by males.

Sites B and C. Similar observations were made at these sites (Figure 3), with large numbers (> 100) of alates and workers clustered in the vicinity of nest entrances, along sandstone walls. A few alate females were also seen among these swarms. Despite persistent attempts by males, no successful worker-male or queen-male matings were recorded. There was a noticeable decline in swarming activity by early afternoon.

Male alates were observed in smaller numbers at several other places on campus, particularly at Sites 1, 2, and 3 (Figure 3). A single, inseminated dealate female was encountered at Site 3 in mid-afternoon, apparently searching for a nest site. During the day, samples of alates were collected from each observation site. Out of a total of 293 alates, 279 (95.2%) were males, and 14 (4.8%) were females.

Later in the evening (10:45 p.m.), lesser numbers of alate males were present, but inactive, on the ground at various locations. Over the next 3 weeks small congregations of males were seen around nest entrances, but never in such numbers or frenzied activity as during the large-scale swarm of 4 October.

The Sydney University population of *chalybaea* consists principally of worker-reproductive colonies, so the preponderance of males among alates is not surprising. The 1976 mating swarms apparently involved insemination of both workers and queens. Only one mated queen was found, however, and it remains unclear if queens mate predominantly in the vicinity of nest entrances or in separate rendezvous sites.

Given the limited number of successful matings observed, it is conceivable that the mating swarm had already passed a peak of activity at the time that observations began (10:15 a.m.). This is also suggested by the absence of workers in a sex pheromone-releasing posture (as described by Hölldobler and Haskins (1977) for *R. metallica*). Such "calling" workers were observed in lab colonies of *chalybaea*, where the behavior occurred both inside and outside the artificial nest. The posture adopted was similar to that described for *metallica* (i.e., head and mesosoma lowered, gaster raised and arched, with tergites exposed). In addition, workers repeatedly rubbed the sides of the gaster with their hind tibiae, presumably facilitating release of pygidial (=tergal) gland pheromone. Such rubbing movements have been reported in *Amblyopone pallipes* queens (Haskins, 1979) but not previously in *Rhytidoponera*.

A mated worker from one of the copulating pairs observed at Site A was isolated in a modified Janet (plaster-of-Paris) nest in the lab and fed on honey and *Drosophila*. On 11 November the first egg was seen, and by 21 December there were 2 eggs, 1 larva and 1 worker cocoon. Just before the colony was terminated, in March, 1977, this mated worker had produced three worker offspring (the first had appeared on 19 January 1977). This is perhaps the first record among the Formicidae of colony-foundation by a lone worker. However, as mentioned previously, there is no evidence that single workers found colonies in the field and it appears that they are always accompanied by an entourage of uninseminated workers.

The inseminated dealate female, also collected on 4 October 1976, was kept under similar lab conditions for five months. The first worker appeared on 7 January 1977. At time of termination

(March, 1977) the colony consisted of 1 queen, 1 worker, 1 worker cocoon, 1 larva and several eggs.

The following spring, in the morning and early afternoon of 1 October 1977 another large mating swarm of *chalybaea* occurred on the University of Sydney campus. As before, this consisted mostly of male alates, concentrated into more or less discrete clusters around several nest entrances. Large clusters were situated at Sites A and C (Figure 3), at exactly the same places observed in 1976. No matings were directly observed, but a timid worker which was being mobbed by males was later found to be inseminated. Workers were generally very aggressive towards males, but the latter persisted in attempts to mate. Once again, samples of alates were collected from various sites, of which 97.0% (195) were males and 3.0% (6) were females. These figures are not significantly different from those of 1976.

On October 12, 1978 small swarms (20–30 individuals) of *Rhytidoponera chalybaea* males were observed at Site C and at several other locations on campus (but not Site A). At 10:15 a.m. males were mostly at nest entrances, apparently in the process of emerging. One alate female was observed; this individual emerged from a nest entrance, and flew off into open sky, ascending rapidly. Similar behavior was observed in males. By 11:30 a.m. many males appeared to be flying into the area, congregations had formed outside nest entrances, and males made repeated attempts to mate with workers.

On the afternoon of the same day two *chalybaea* queens (one alate, one partially dealate) were seen floundering on the sidewalk in a heavily built-up section of downtown Sydney. Both were uninseminated. This suggests that alate females may disperse a considerable distance before mating.

Colony Structure and Life Cycle

In most populations of *confusa*, *chalybaea*, and *impressa*, queen-right and worker-reproductive colonies coexist, in intermediate proportions. Despite the likely disparity between mating sites of winged queens and workers, genetic data from electrophoretic studies (Ward, 1978, 1980) reveal no indication of extensive inbreeding or assortative mating with respect to colony type. This is consistent with the observation that brood development and alate production proceed at similar rates in the two colony types, and that

release of alates in worker-reproductive colonies occurs synchronously with (or at least in the same season as) queenright colonies.

As for the remaining species in the *impressa* group, only queenright nests are known in *purpurea* and this species shows a brood development pattern similar to the three others. By contrast, distinct winged queens are unknown in *enigmatica* (all recorded colonies worker-reproductive), and this species diverges from its closely related congeners by releasing most alates in the fall, although males were found overwintering in one nest. The limited information indicates a possible relaxation of synchrony in the release of ergatoid-seeking male alates, a pattern which would be predicted with the loss of the winged queen caste, especially if the sexual calling behaviour of ergatoid gynes is temporally dispersed. This trend is continued in some other *Rhytidoponera* species outside the *impressa* group, in which functional queens are rare or absent, and flights of alates (males) are reported to be highly non-specific with respect to season (Brown, 1958; Haskins & Whelden, 1965; Haskins, 1979). However, since most of the data come from lab colonies of one species (*metallica*) additional field observations are desirable.

Scattered collections of colonies from different times of the year may give a misleading impression of patterns of alate production. In at least two species of the *impressa* group, alates can be found in some nests from February to November. Although this superficially suggests aseasonal production of alates, a detailed examination of brood development demonstrated that only one crop of alates is produced each year and that alates are released over a limited time period. Additional field studies are necessary to determine whether brood development in *Rhytidoponera* species without queenright colonies is less constrained by the need for synchronous alate release. For comparison with the *impressa* group, such studies would be most appropriately directed towards other species of east Australian mesic forests, in order to minimize climatic and other environmental differences.

SUMMARY

In the *Rhytidoponera impressa* group there are two kinds of colonies, which are distinguished by the type of reproductive female present: queenright colonies with a single dealate queen, and

worker-reproductive colonies in which one or more mated "workers" occur in lieu of a queen. It appears that worker-reproductive colonies normally reproduce by colony fission or budding, although information on this process is fragmentary. Queenright colonies are founded by lone queens. Colony-founding queens are most frequently encountered in the spring and early summer; such queens leave the brood chamber to forage for food.

In mature colonies of *confusa* and *chalybaea*, the development of brood and production of alates is highly seasonal (and essentially similar for both queenright and worker-reproductive colonies). One crop of workers and alates is produced each year, the former eclosing from cocoons between January and June, the latter between February and April. Most or all alates overwinter in the nest (along with small to medium-sized larvae), and are released in the spring (September–November). Similar seasonal patterns are shown by *impressa*, *purpurea* (in Australia), and *enigmatica*, except that colonies of *enigmatica* generally do not retain alates over the winter.

In the population of *chalybaea* on the University of Sydney campus, mating flights took place in early October for 3 consecutive years. During these flights, flying males became concentrated into clusters around nest entrances where they attempted to mate with workers, with males, and with the occasional alate female. Several worker-male but no queen-male matings were observed in these nest-associated swarms. Like males, queens appear to disperse some distance before mating, and possibly utilize mating sites other than nest entrances.

ACKNOWLEDGEMENTS

This work was supported by an Australian Commonwealth Scholarship. Additional support from L. C. Birch and the University of Sydney is gratefully acknowledged. I thank D. Feener and A. Forsyth for comments on the manuscript.

REFERENCES

BROWN, W. L.

1953. Characters and synonymies among the genera of ants. Part I. *Breviora*, 11, 1–13.

1954. Systematic and other notes on some of the smaller species of the ant genus *Rhytidoponera* Mayr. *Breviora*, **33**, 1-11.
1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bull. Mus. Comp. Zool. Harvard*, **118**, 175-362.
- HASKINS, C. P.
1979. Sexual calling behavior in highly primitive ants. *Psyche*, **85**, 407-415.
- HASKINS, C. P. AND W. M. WHELDEN
1965. "Queenlessness", worker sibship, and colony versus population structure in the formicid genus *Rhytidoponera*. *Psyche*, **72**, 87-112.
- HÖLDOBLER, B. AND C. P. HASKINS
1977. Sexual calling behavior in primitive ants. *Science*, **195**, 793-794.
- WARD, P. S.
1978. Genetic variation, colony structure, and social behaviour in the *Rhytidoponera impressa* group, a species complex of ponerine ants. Ph.D. Thesis, University of Sydney.
1980. Genetic variation and population differentiation in the *Rhytidoponera impressa* group, a species complex of ponerine ants (Hymenoptera: Formicidae). *Evolution*, **34**, 1060-1076.
1981. Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae). 1. Habitats, nest sites, and foraging behavior. *Psyche*, **88**: 89-108.